

Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*

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In the suricate (*Suricata suricatta*), a cooperatively breeding mongoose, one individual typically watches out for predators while the rest of the group is foraging. Most of the time these sentinels announce their guarding duty with special vocalizations. The response of foraging group members to these calls was investigated by analysing observational data, and by performing playback experiments. The use of special calls by sentinels, and the responses of the foraging group members to them, suggest that the coordination of vigilance is strongly influenced by vocal communication. Sentinel calls decreased the time spent alert by the foraging group members. Other group members were less likely to go on guard when a sentinel was vocalizing. Both the proportion of time during which guards overlapped, and the proportion of time the group was unprotected without a guard, decreased when sentinels announced their duty, due to better coordination of the rotation of sentinels. Suricates, however, do not appear to use sentinel calls to mediate a strict rotation of guarding duty.

Keywords: sentinel calls; sentinels; vigilance; cooperative breeding; suricates

1. INTRODUCTION

Vigilance behaviour in some social bird and mammal species is coordinated by sentinel systems, in which individuals take turns in watching for predators, while the rest of the group is foraging (for a review, see Bednekoff 1997). It has been suggested that such behaviour allows each foraging member to decrease its own vigilance and gain additional time to search for food (McGowan & Woolfenden 1989; Bednekoff 1997). However, Ward (1985) pointed out that in bird flocks the costs of coordinating vigilance exceeded the potential benefits. He argued that birds have to interrupt their foraging to check visually for a guard on duty. Wickler (1985) observed that in various babbler species, coordination of vigilance may be independent of visual scanning because guards announced that they were on duty using a particular vocalization, the 'watchman's song'. Bednekoff (1997) suggested that while the vocalization of guards might make sentinel systems run more smoothly, it is not a necessary condition for the evolution of sentinel behaviour. Goodwin's definition (Goodwin 1976; McGowan & Woolfenden 1989) of true sentinel behaviour requires interaction between the guards and those being protected; vigilant individuals guard others and alert them to danger, and the individuals take turns in guarding. Therefore, special sentinel calls to announce vigilance may not be essential for a sentinel system, but they might increase its efficiency. This may become especially important in animals living in habitats which do not permit a clear view of the sentinel, because vocal announcement of guarding would eliminate the necessity for foraging members to check

visually for a sentinel (Metcalf 1984; Rasa 1986). Vocalizations to announce guarding duties have also been described in other species including the Florida scrub jay, *Aphelocoma coerulescens* (McGowan & Woolfenden 1989), the white-browed sparrow weaver, *Plocepasser mahali* (Ferguson 1987), the dwarf mongoose, *Helogale parvula* (Rasa 1986) and the suricate, *Suricata suricatta* (Moran 1984; Macdonald 1992; Doolan 1997).

Wickler (1985) described watchman's calls in several babbler species as being calls of short duration and soft amplitude that were emitted continuously over the whole guarding period. Dwarf mongooses also announce their guarding continuously by emitting a loud version of contact calls (Rasa 1986). For other species, such as the white-browed sparrow weaver (Ferguson 1987), or the Florida scrub jay (McGowan & Woolfenden 1989), calls of sentinels are only given infrequently at the beginning or end of a guarding session, but nevertheless have been suggested to have some function announcing sentinel duty.

Vocal announcement of a sentinel on duty may not only allow the foraging members to decrease their vigilance, but could also help to coordinate guarding behaviour between the group members. In dwarf mongooses, group members rotate their guarding in a regular pattern in which each individual takes over from a particular member of the group (Rasa 1986). Rasa suggested sentinel calls informed the foraging individuals about the guard's identity and location, and further enabled the sentinels to rotate without overlapping their vigilance periods.

Suricates are cooperatively breeding mongooses living in open semi-desert areas in packs of between three and 25 members, consisting of adults, subadults and dependent young (Doolan 1996a,b; Clutton-Brock *et al.*

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1998a). A group forages together, and they often have a sentinel watching out for predators (Moran 1984; Doolan 1997). On the majority of occasions, sentinels announce their guarding vocally, but sometimes remain silent (Macdonald 1992; Doolan & Macdonald 1997). Suricates dig in the sand for food, and regularly interrupt their foraging to scan for predators, or to check if another individual is on guard. When a sentinel is announcing its duty, the foraging members may decrease their vigilance and hence interrupt their foraging less frequently. In a species that digs for mobile prey in the ground, this could substantially increase foraging success.

In this paper, I describe the vocalizations of sentinels in suricates and their effect upon foraging group members. First, I show that the sentinel system in suricates is effective in detecting predators. I then describe sentinel vocalizations and examine whether these calls are emitted continuously over the whole guarding period. Furthermore, I investigate the response of foraging members to the calls, and ask (i) do foraging members decrease their own vigilance when they hear sentinel calls? (ii) are foraging individuals less likely to go on guard in response to sentinel calls? (iii) does the coordination of guarding improve? and (iv) do suricates use sentinel calls to mediate the rotation of sentinel duty?

2. METHODS

Data on sentinel vocalizations were collected from six different groups in the Kalahari Gemsbok National Park, South Africa, along the dry Nossob river-bed (Clutton-Brock *et al.* 1998b), from a total of 42 different individuals. For most of the analysis, however, sufficient data were only available from four groups. Group size varied from four to 20 members in total, including dependent offspring. The members of the groups could be recognized individually and were habituated to the point where I could walk with them and make recordings from 50 cm. Calls were recorded using a SonyTM digital audio tape recorder DAT Pro II TCD D10 and a SennheiserTM directional microphone MKH 816. Playbacks were performed with a SonyTM DAT recorder connected to a SonyTM Walkman loudspeaker SRS A60. Spectrograms were analysed with the Kay Sonagraph Analyser, Model 5500, using a 150 Hz wide band set-up (Kay Elemetrics Corp. 1989, Pine Brook, NJ, USA).

(a) *Sentinel behaviour*

To determine whether sentinel calls have a vigilance function I first investigated whether sentinels in suricates followed the definition proposed by Goodwin (1976), by warning other individuals of danger. The alarm call frequency of individuals when foraging and when guarding were compared. Any suricate going on raised guard on an elevation higher than 10 cm was considered as a sentinel, while any other individual was taken as foraging. Whenever an alarm call was given the identity of the caller was recorded as well as its behaviour, categorized either as sentinel duty or foraging.

(b) *Sentinel vocalization*

Whenever an individual went on raised guard, its identification, the duration of the guarding period, and whether it had been vocalizing at any stage (if possible) were recorded. I recorded the types of vocalization emitted over the entire guarding period for a total of 60 guarding sessions of 24

different individuals. This enabled me to compare the calls used by different individuals and the change in the calling pattern over time. Furthermore, I analysed sonograms of the calls of 12 individuals from four different groups to compare the structure of calls used by different individuals within and between groups.

(c) *Response of foraging members to sentinel vocalization*

(i) *Vigilance of foraging members*

The response of foraging members to sentinel calls was investigated by analysing observation data, and by performing playback experiments. I tested whether the time foraging individuals spent alert decreased when a sentinel was vocalizing, and also how frequently they went on guard during periods when a sentinel was vocalizing in comparison with when it was quiet. The influence of sentinel vocalizations on the rest of the group was also tested by playing back the calls to a foraging individual when there was no sentinel. The vocalization of a guarding individual was recorded and then broadcast to foraging suricates in the same group ($n=4$ groups), following an individual at a distance of 3–5 m with a small Walkman loudspeaker at a height of 80 cm. The behaviour of the target suricate was recorded on a PSIONTM datalogger, Organizer II, Model L264, concentrating on the time spent foraging and alert (including looking up, guarding on the ground and raised guard). Two control sessions of half an hour each were conducted: one in which background noise (recorded in the field without disturbances by birdsong or other animals calling) was played, and the other in which contact calls of a member of the same group were played. This was repeated once for all the different test periods, giving a total of a 1 h experiment and a 1 h control session. To avoid an order effect, the experiment and the control periods were conducted alternately. If, during the test or control period, another member of the group went on guard (raised guard or guard on ground with vocalization), the data recording was interrupted to make sure that the vocalization was responsible for the effect, and not the view of a sentinel.

(ii) *Probability of going on raised guard*

To test whether having a guard and hearing sentinel vocalizations decreased the frequency of other individuals going on raised guard, I compared observational data from four groups for three different periods: (i) when no sentinel was up, (ii) when a sentinel was up but not vocalizing, and (iii) when a sentinel was up and emitting the guarding calls. In the first case, with no sentinel on guard, I calculated the average time it took for an individual to go on guard since the last sentinel had left its position. For the other two periods, when a sentinel was up without vocalizing or with vocalizing, I calculated the time from when a sentinel had taken its position until the next individual went on guard. From the 12 playback experiments, it was also possible to estimate the average time between guards when the suricates heard the sentinel vocalization, but did not see a guard up.

(iii) *Probability of terminating raised guard*

Observational data were also used to investigate whether the probability of a guarding session terminating depended on whether a sentinel was vocalizing. I measured the duration of overlapping guards, documenting the time which lapsed between a second individual going on guard and the first sentinel leaving its position, and resuming foraging again. In

addition, I tested whether vocalizations from either the first or second sentinel influenced which individual stayed on guard.

(iv) *Coordination of guarding*

I was then able to estimate the influence of vocal announcement of sentinel duty on the coordination of guarding behaviour and the increase in foraging time from observational data. I compared foraging periods when sentinels vocally announced their duty and when they kept silent, by looking at the amount of time that (i) one sentinel was up, (ii) there was more than one sentinel, and (iii) no sentinel was up. Foraging periods coordinated by sentinels vocalizing included all sessions when one or several sentinels were on duty and at least one of them calling. In addition, the periods after a vocalizing sentinel had left, but no other individual was on guard, were summed, and the percentage of the whole period covered by a sentinel calculated. Whenever a sentinel went on guard without calling it was counted as a period of silent sentinels, as was the time after that guarding session until another individual went on guard and announced its duty again. This was done for all the observation periods per group, and the mean time was standardized to 1 h foraging time.

(b) *Rotation of guarding*

To investigate whether suricates use sentinel calls to coordinate the rotation of guarding, I tested whether certain individuals went on guard predominantly after a specific individual. In four groups I analysed the sequence of the different individuals in a group going on sentinel duty.

(c) *Statistics*

Almost always non-parametric tests were used because the sample sizes were small (Zar 1984). U indicates a Mann–Whitney test, Z a Wilcoxon signed-rank test, H a Kruskal–Wallis test and a chi-square or a Friedman test. In some comparisons, such as the probability of going on raised guard, I performed a Mann–Whitney test by using the group as an independent data point ($n = 4, 4$), rather than conducting a Wilcoxon test on the level of each experiment, since this would have included repeated measures on the same group. In my analysis testing the influence of sentinels vocalizing and the duration of guard on the probability of terminating sentinel behaviour, I performed an ANOVA with repeated measures and quote the F -value. All p -values given are two-tailed. The error bars in the figures show inter-quartile ranges, and the circles denote the ranges.

3. RESULTS

(a) *Sentinel behaviour*

Sentinels in suricates appear to look out for predators and warn other group members in case of danger by alarm calling. The same individual on sentinel duty gave alarm calls more often than when it was foraging (alarm call rate on sentinel duty: 0.86 ± 0.13 calls h^{-1} ; while foraging: 0.08 ± 0.01 calls h^{-1} ; Wilcoxon test: $Z = -5.704$, $n = 48$, $p < 0.001$).

Furthermore, the efficiency of predator detection improved when a sentinel was up. Suricates acting as sentinels called alarms to potential predators in 77% out of all predator detections by sentinels when they were more than 150 m away, compared with foraging individuals which only emitted 44% out of all their alarm calls

to predators at this great distance (chi-square: $\chi^2 = 10.31$, d.f. = 1, $p = 0.0013$).

(b) *Sentinel vocalization*

Suricate sentinels announced that they were on duty with special vocalizations. For 55% of the time foraging suricates had a guard on an exposed lookout. Guarding individuals spent 80% of their time vocalizing. In total, six different calls, in addition to alarm calls, were emitted by sentinels (figure 1). The four most frequently given sentinel calls (> 95% of all emitted sentinel calls) consisted of a single or multiple note of short duration and these calls were only audible to the human ear up to a distance of 15–20 m. The two less common sentinel calls were of longer duration and might function to alert other individuals. However, this has still to be tested. The same vocalizations ($n = 4$: single, double, triple and multiple note) significantly differed between individuals in duration (Kruskal–Wallis: $H = 35.55$, d.f. = 11, $p = 0.0002$) and fundamental frequency (Kruskal–Wallis: $H = 35.73$, d.f. = 11, $p = 0.0002$), and seemed not to be a group characteristic (table 1). Each member had its own call characteristic, having both a consistent call duration (Friedman test: $\chi^2 = 1.41$, d.f. = 2, $p = 0.49$) and fundamental frequency (Friedman test: $\chi^2 = 0.18$, d.f. = 2, $p = 0.91$) in their three most frequently emitted guarding calls (single, double and triple note call, 81% of all sentinel calls observed).

Sentinels changed their calling frequency over a guarding period. Individuals began to vocalize from the beginning of a period. The number of calls given in the first two minutes of acoustically announced guards was on average 19.8 ± 14.3 ($n = 24$ individuals). Vocalization ceased sometime before the individual left its guarding position (Friedman test: $\chi^2 = 27.7$, d.f. = 4, $p < 0.0001$, $n = 24$ individuals) (figure 2). No terminal call was observed. In most cases the individual leaving its guarding position immediately gave contact calls, either while descending or as soon as it began to forage again.

(c) *The influence of sentinel calls on the foraging members*

(i) *Vigilance of foraging members*

Playing back sentinel calls to foraging members reduced their alertness. In 12 experiments, in which sentinel calls were played to a foraging member when there was no individual on guard, the time the target individual spent vigilant substantially decreased compared with the control period (Wilcoxon: $Z = -3.06$, $n = 12$, $p = 0.002$) (figure 3). In the additional control experiment when the influence of contact calls was tested on foraging individuals, the proportion of time spent vigilant did not differ markedly between the control and experimental sessions (Wilcoxon: $Z = -0.52$, $n = 6$, $p = 0.60$).

(ii) *Probability of going on raised guard*

At times when there was already a sentinel up, the other members in the group were less likely to go on raised guard. The analysis of the time interval between guards in four groups showed a significant difference for the three different conditions, when there was (i) no sentinel, (ii) a quiet sentinel, and (iii) a sentinel vocalizing.

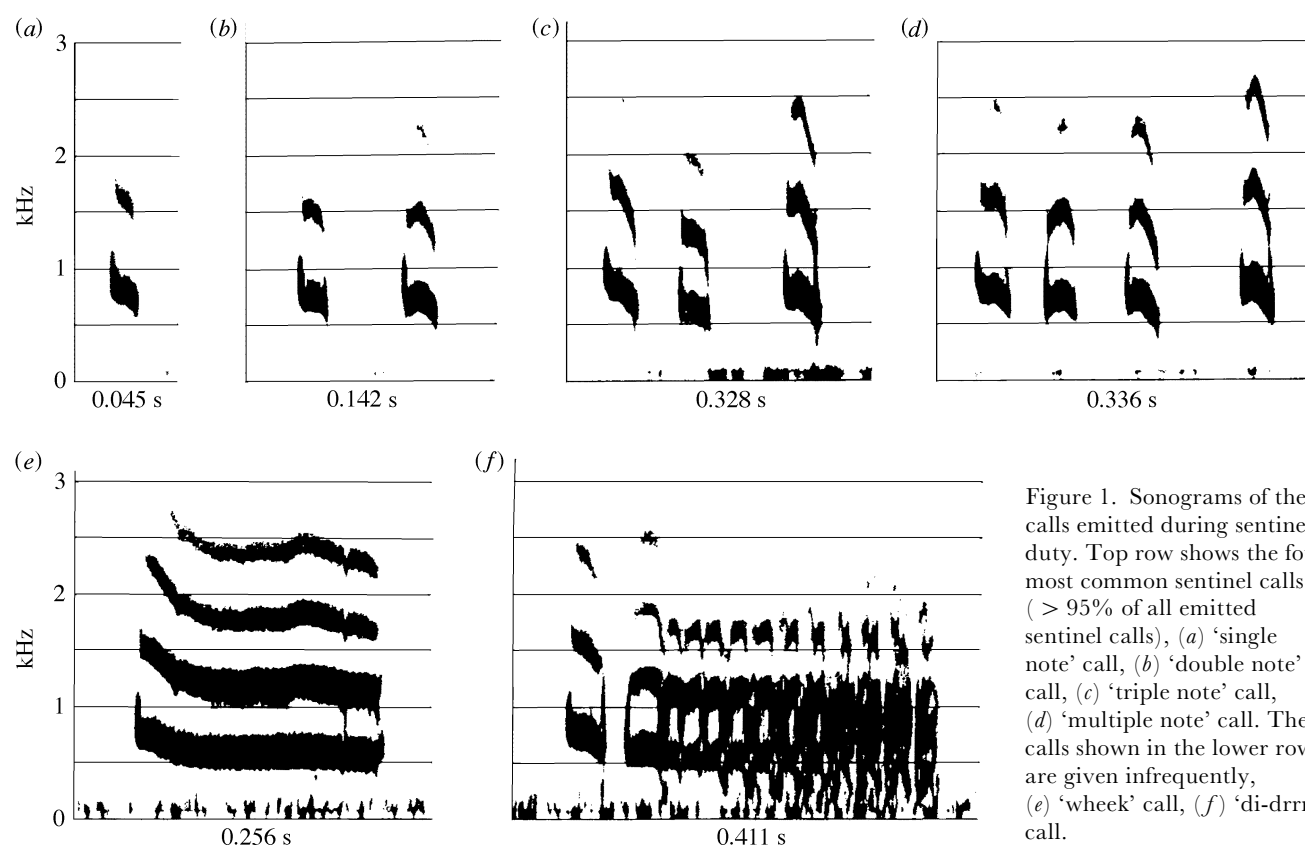


Figure 1. Sonograms of the calls emitted during sentinel duty. Top row shows the four most common sentinel calls (> 95% of all emitted sentinel calls), (a) 'single note' call, (b) 'double note' call, (c) 'triple note' call, (d) 'multiple note' call. The calls shown in the lower row are given infrequently, (e) 'wheel' call, (f) 'di-drrr' call.

Table 1. *Fundamental frequency and duration (mean) of the most frequently used sentinel calls for several individuals with different status and sex from four groups*

(sn, single note call; dn, double note call; tn, triple note call; mn, multiple note call with greater than three notes per call; sub, subordinate; dom, dominant. In the case of the double and triple note call, only the fundamental frequency and duration of the first note were considered.)

sex	status	group	fundamental frequency (Hz)				duration of first note (ms)			
			sn	dn	tn	mn	sn	dn	tn	mn
male	sub	A	1040	992	960	960	26.7	28.4	26.0	28.5
male	dom	A	792	792	808	800	59.2	55.8	55.6	58.0
male	sub	A	1000	1010	1000	1020	39.6	40.4	40.8	42.2
female	dom	J	1010	960	1040	1020	43.2	45.5	42.0	48.1
male	dom	J	768	760	760	820	45.4	47.3	42.0	44.0
female	sub	J	1100	1112	1120	—	43.0	44.6	41.5	—
male	sub	J	1120	—	—	—	59.0	—	—	—
female	sub	N	980	1000	920	—	36.0	41.0	43.0	—
female	sub	N	780	770	807	840	34.3	30.6	32.0	39.0
male	dom	N	740	744	752	—	46.0	46.2	46.0	—
female	dom	S	880	887	880	880	53.0	52.3	54.0	56.0
male	sub	S	1080	1144	1107	—	28.3	30.8	32.7	—
female	sub	S	800	773	—	—	42.0	43.0	—	—

The time interval until the next individual went on raised guard rose substantially when there was already a sentinel up, and increased even more when the sentinel was emitting calls (Kruskal–Wallis: $H_{4,4} = 8.77$, $p = 0.013$, $n = 4$ groups) (figure 4a).

The longer interval between individuals going on guard when a sentinel was vocalizing than when it kept silent, could be explained by the fact that announced guards in general tended to be longer than guards where individuals did not emit sentinel calls (Manser *et al.* 1999).

However, the playback experiments of sentinel calls confirmed the result in that the time between guards increased from the control period with background noise to the test period with sentinel calls (Mann–Whitney: $U = 16.0$, $p = 0.03$, $n = 4,4$ groups) (figure 4b). The experiment was conducted three times in each of the four different groups, and the mean value per group was used as the independent data point.

The interval between guards when no sentinel was up was shorter during the observational periods than

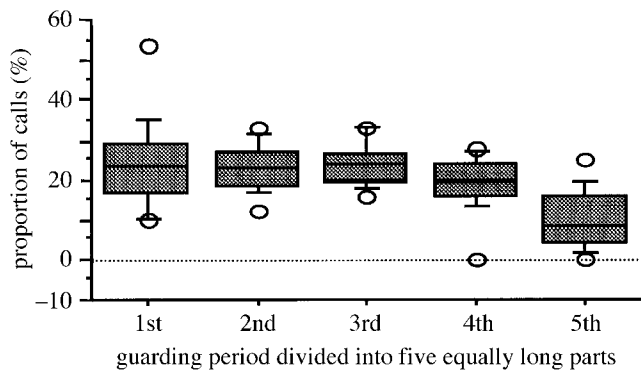


Figure 2. Proportion (per cent) of sentinel calls given in the different parts of a guarding session. The box plots show 10th, 25th, 50th, 75th and 90th percentiles. The circles denote ranges.

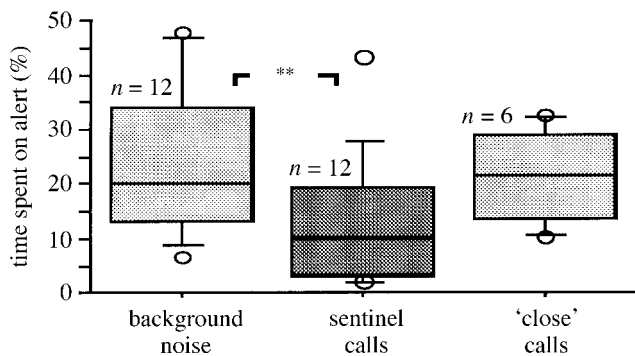


Figure 3. Time spent alert per hour of foraging period in the control and test periods. The box plots show 10th, 25th, 50th, 75th and 90th percentiles. The circles denote ranges (** = $0.01 > p > 0.001$).

in the playbacks. This apparent discrepancy arose because experiments were conducted at times when individuals were not going on raised guard very often, so that it would be clear that group members were responding to the playback, and not to the sight of a sentinel on duty.

(iii) Probability of terminating raised guard

The vocalizations of sentinels were associated with the probability that they would stop guarding. When another individual went on guard, sentinels emitting calls did not terminate their guarding as fast as non-vocalizing sentinels. The average time a sentinel stayed on guard when another individual went up was always longer for vocalizing sentinels than silent sentinels, independent of the duration a sentinel had already been up (ANOVA with repeated measures: $F_{1,20} = 67.36$, $p = 0.0004$).

Whether a sentinel already up left its position when a second individual went on guard depended less on whether the first sentinel was vocalizing than on whether the second sentinel began to emit calls. If the second sentinel was silent, it stopped guarding before the first sentinel in 74.3% of cases (total $n = 316$ guarding periods). If the second guard vocalized, on the other hand, it terminated its guard before the first sentinel in only 32.6% of cases (chi-square: $\chi^2 = 53.35$, d.f. = 1, $p < 0.0001$). This was independent of whether the first sentinel was vocalizing (chi-square: $\chi^2 = 0.52$, d.f. = 1, $p = 0.47$).

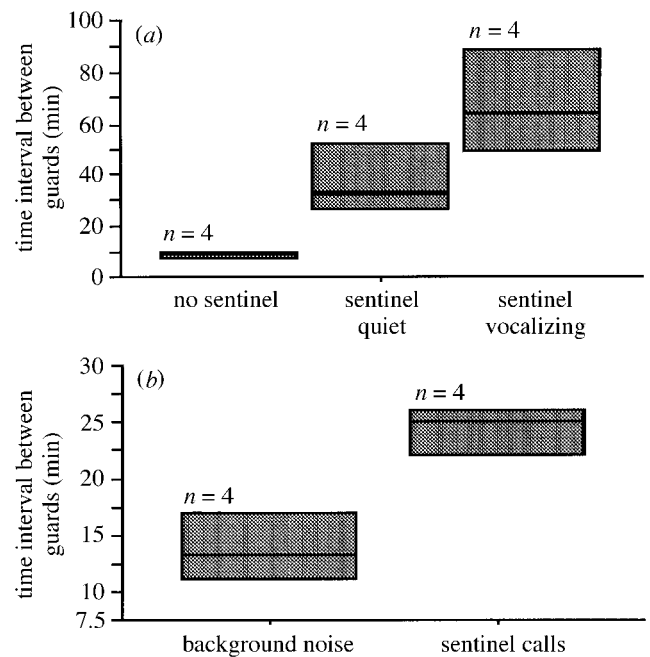


Figure 4. (a) Time interval between guards during foraging depending on whether there was (i) no sentinel up, (ii) a sentinel without vocalizing, and (iii) a sentinel emitting calls. The box plots show 25th, 50th and 75th percentiles. (b) Time interval between guards when playbacks of (i) background noise, and (ii) sentinel calls were broadcast. The box plots show 25th, 50th and 75th percentiles.

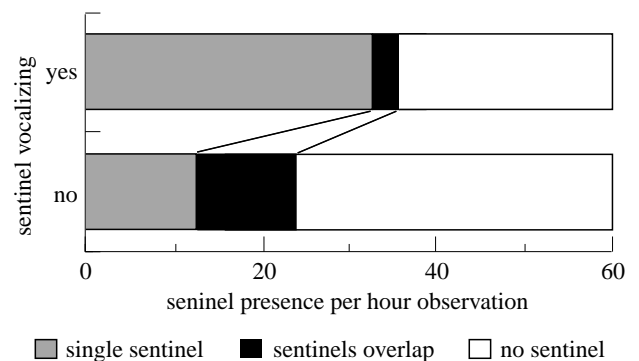


Figure 5. Proportion (median) of protected and unprotected time per hour of foraging when the sentinel was vocalizing or not.

(iv) Coordination of guarding

The vocalizations of a sentinel influenced the coordination of guarding behaviour within the group (figure 5). The mean duration of guarding periods was longer if the sentinel vocalized (duration: median = 8.42 min, interquartile range (IQR) = 1.89), than if it did not (duration: median = 3.4 min, IQR = 1.13; Mann-Whitney: $U = 16.0$, $n = 4,4$, $p = 0.02$). The unprotected time between guarding attempts decreased slightly, but not significantly if the previous sentinel had been vocalizing (silent: median = 12.9 min, IQR = 4.56; vocalizing: median = 8.7 min, IQR = 1.73; Mann-Whitney: $U = 10.0$, $p = 0.56$, $n = 4$ groups). Even though the overlapping time per guarding attempt was longer when the sentinel was vocalizing (median = 3.28 min, IQR = 1.45) compared with when it was quiet (median = 2.62 min, IQR = 1.83), there was a

shorter relative overlap when vocalizing, because the guard duration was more than 2.5 times longer for a vocalizing sentinel than for a quiet sentinel. Whether a sentinel emitted calls or not, an immediate turnover of guarding in which there was no overlap between sentinels happened in about 10% of observed guarding periods. Guards overlapped in 30% of their guarding periods when the sentinel was quiet and in only 20% of guarding periods when the sentinel was announcing its duty (Mann–Whitney: $U=16.00$, $p=0.02$, $n=4$).

Overall, this resulted in better coordination during times when sentinels vocalized, as the total protected time for the foraging group increased (quiet: median = 23.82 min h^{-1} , IQR = 6.52; vocalizing: median = 36.18 min h^{-1} , IQR = 6.52; Mann–Whitney: $U=16.0$, $p=0.02$, $n=4$), and the overlap of sentinels decreased (quiet: median = 11.5 min h^{-1} , IQR = 4.36; vocalizing: median = 3.66 min h^{-1} , IQR = 2.0; Mann–Whitney: $U=16.0$, $p=0.02$, $n=4$) as shown in figure 5 for a 1 h foraging period.

(d) *Rotation in guarding behaviour*

In none of the four tested groups was a pattern found where certain individuals predominantly took over from a specific individual. A log-likelihood ratio analysis showed that there was no strong evidence of non-random associations (group 1: $G=19.2$, d.f. = 25, $p=0.8$; group 2: $G=14.5$, d.f. = 9, $p=0.1$; group 3: $G=26.3$, d.f. = 25, $p=0.4$; group 4: $G=49.3$, d.f. = 81, $p=0.99$).

4. DISCUSSION

The use of special vocalizations by sentinels, and the response to them by foraging members, suggest that the coordination of vigilance behaviour in suricates is strongly influenced by auditory communication. Sentinels in suricates announced most guards by special short, soft calls. Foraging individuals showed a significantly lower level of vigilance in response to playbacks of sentinel calls than to playbacks of background noise or contact calls. During periods in which sentinels announced their duty, the coordination of their guarding rotation also became more efficient. Suricates, however, do not use sentinel calls to mediate the rotation of guarding duty.

In suricates about 55% of foraging time was protected by having a sentinel on guard. During 80% of this guarding time the sentinels announced their duty vocally. When sentinels were vocalizing, not only did the coordination of the guarding system increase, but so did the time spent foraging by each individual, as they interrupted their activities less often to scan their surroundings. Thus, vocalizations improved the efficiency of the suricate sentinel system. On the other hand, the guarding bouts without vocalizations confirm Bednekoff's suggestion that vocalizations might help to run sentinel systems more smoothly, but they are not essential for sentinel systems to evolve (Bednekoff 1997). However, for a species such as the suricate, living in a harsh environment with limited food resources and high predation risk, a 10% increase of foraging time, and a likely higher rate of foraging success, because they do not have to interrupt foraging bouts to scan for predators, may have a large impact on reproduction and survival (Clutton-Brock *et al.* 1998a).

Although the vocalizations emitted by sentinels included information about their identity, suricates seemed not to use this information to mediate the rotation of their guarding. The four most frequently used sentinel calls were consistent for each individual in fundamental frequency and duration, but differed between group members. This would allow individual recognition by calls. Rasa (1986) suggested that the dwarf mongoose may use the recognition of individuals by calls to coordinate the rotation of the guarding period. No such regular pattern of an individual taking over predominantly from one particular individual was observed in suricates, and other factors, such as foraging success, might be more likely to influence the guarding rotation (Clutton-Brock *et al.* 1999; Manser *et al.* 1999). Instead of using the information about the identity of a guard to coordinate the rotation, they might use it to estimate the quality of a guard, e.g. reliable versus unreliable sentinels. This has yet to be tested.

An acoustically coordinated sentinel system, such as that in suricates, substantially increases foraging time for the group members when compared with a system where a guard must be visually located. The advantages seem especially obvious in social foraging groups moving in search of food on the ground, through habitat with poor visibility (Rasa 1986). Acoustical announcement of sentinel duty might be less important for pair-living species, such as klipspringers, *Oreotragus oreotragus* (Tilson 1980), where only the partner is guarding and its position is easy to localize. This would also apply to species foraging in open fields, as described for vervet monkeys, *Cercopithecus aethiops* (Horrocks & Hunte 1986). Benefits of vocalizing are also restricted to groups that forage close together, as they remain within hearing range.

The evolution of continuous announcement of sentinel duty offers a simple system to coordinate the vigilance behaviour among all individuals in a group. As long as foraging individuals hear sentinel calls they know somebody is guarding and can decrease their own vigilance. When they do not hear sentinel calls any more, either there is no guard or the current guard is about to leave its position and has to be replaced. It seems unlikely that a system where individuals just announce the beginning or the end of their guarding periods (McGowan & Woolfenden 1989) would be as efficient under such circumstances, as the chance of missing those signals, as a receiver moves through dense habitat, might be very high.

I thank the National Parks Board, South Africa, for permission to work in the Park and, in particular, Dries Engelbrecht, warden of the Kalahari Gemsbok Park, as well as the Park staff based at Nossob, including rangers J. Herrholdt and G. de Kock. The members of the Mammal Research Institute, University of Pretoria, including Professor J. Skinner and M. Haupt, were a big help in logistical questions. I am most grateful for T. H. Clutton-Brock's supervision. P. Brotherton, D. Gaynor, R. Kinsky and J. O'Riain contributed not only to data collection in the field, but also to useful discussions. Several volunteers made substantial contributions to the work (L. Postgate, H. Nicholls, K. McKay, P. Dixon, R. Smith, C. McLeod and A. Toole). Thanks to three anonymous referees for their comments and L. Sharpe and S. White for proofreading. The research was funded by grants given to M.B.M. from the Roche Research Foundation, Basel; Freiwillige Akademische Gesellschaft, Basel; and the

Royal Society, London, as part of an exchange programme with the Swiss Nationalfonds, Janggen-Poehn St Gallen, Pentapharm AG Aesch, Zoological Institute, Basel, and a loan from Clare College Cambridge and the University of Basel.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.

